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THE ORIGIN AND CLASSIFICATION OF THE APTERYGOTA.¹

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Very early in the study of insects, theories as to their origin began to crystallize, and as far back as 1869 Brauer formulated a theory that insects were evolved from lower arthropods through forms similar to the species of *Campodea*. These early theories were formed long before our knowledge of insect morphology was sufficiently complete to give the proper basis of facts for any sound theory. Also several of the primitive arthropod groups known to us today were little known then or had not yet been discovered.

MORE RECENT THEORIES OF THE ORIGIN OF INSECTS.

Three of the theories advanced relating to the origin of insects have had a considerable following up to the present. They are here considered.

(a) The Crustacean Theory, which at one time probably was the most acceptable of all, has been especially upheld by such entomologists as Hansen (1893), Carpenter (1903), and Crampton (1916, 1919, 1922). Exponents of this theory claim to be able completely to homologize the mouth parts of such primitive insects as the thysanurans with those of the crustaceans of the group Malacostraca. Also the parts of the most outstanding crustacean morphological structure, the biramus limb, are homologized with parts of the head appendages as well as with those of the abdominal appendages.

The weakest point to be found in the Crustacean Theory is our inability properly to homologize the internal organs of Insecta with those of Crustacea. Furthermore, the vestigial abdominal appendages of primitive insects, together with their accompanying basal sclerites and closely associated sacs or glands, fit into an almost continuous intergrading system with those of certain primitive groups of land arthropods.

Tillyard (1930) pointed out the difficulty of deriving the

¹ Address of the retiring president of the Society, delivered at the February meeting, 1942.

insectan type of reproductive system from that of the Crustacea. The Insecta and Crustacea are even more divergent in regard to their excretory systems. This system in most of the crustaceans consists either of the antennal glands, which open on the bases of the antennae, or the maxillary "shell-glands," which open on the bases of the second maxillae. These glands represent modified nephridia, and open to the exterior, having no connection with the alimentary canal. They are structures vastly different in origin and relationships from the malpighian vessels of insects. However, in some of the amphipod crustaceans either single or paired caeca, having an excretory function, open into the posterior end of the mesenteron. Their position and structure indicate that, while they probably are not homologous with the malpighian vessels of insects, they are suggestive of such and possibly may be considered as forerunners of malpighian vessels.

(b) The Protaptera Theory of Tillyard (1930) calls for a hypothetical ancestral group from which the Insecta, the Progoneata, and the Opisthgoneata are derived and continued as three distinct lines of descent. This hypothetical group is called the Protaptera, and was supposed to have paired gonads on postcephalic body segments IV to VIII. In presenting his theory Tillyard has given an interesting review of some of the different theories of the origin of insects, and has pointed out very effectively some of the weaknesses of each.

Imms (1936), in addition to calling attention to certain discrepancies and statements that are "obviously incorrect" in Tillyard's paper, in one sentence states this chief objection to the theory: "The theory of Tillyard, which formulates an oligomerous protomorphic ancestor, has resulted in an attempt to trace the origin of insects much farther back in the evolution of arthropods than the evidence of comparative morphology and embryology appears to justify."

To this criticism should be added another relating to the evidence presented in the consideration of the evolution of the arthropod leg. Tillyard's conclusion not only is based upon an insufficient study of leg segmentation, but, because the musculature of the legs was not studied, subsegments were frequently confused with true segments, and the composition and identity of certain segments were not properly detected. Thus Tillyard regarded the leg of Symphyla and Collembola as being identical in segmentation, each being composed of four segments, not counting the pretarsus, and in each group the distal segment was regarded as the tibiotarsus. Yet the writer (Ewing, 1928) had previously shown from a study of the musculature of the legs in these two groups that in the symphyliid leg there are five movable segments in addition to the immovable subcoxa, and that the tibia and tarsus are distinct. Further, it should

be stated that in regard to the collembolan leg there is much variation in its segmentation. While the leg is commonly four segmented (not counting the subcoxa or the pretarsus), and possibly has the tibia and tarsus fused into a tibiotarsus, it may be five-segmented, possessing either two trochanters or a freely articulated tibia and tarsus.

Again, according to Tillyard (1930) the leg in the Thysanura is either seven or eight segmented (counting subsegments) while in most of the pterygota it was regarded as nine-segmented. Actually, however, the legs of most of the Machilidae and Lepismatidae are identical in segmentation with those of the generalized type for the Insecta, being composed of a coxa, trochanter, femur, tibia, a tarsus of three subsegments, and a pretarsus. This point has been made clear by a study of the musculature of the legs (Ewing, 1928).

Tillyard's explanation of the evolution and variation of the tracheal system is particularly interesting. He points out that the original terrestrial arthropods probably had no tracheae but breathed through their cuticle. This apparently is in accordance with the evidence. Particularly it should be noted that in the primitive group Pauropoda there are no tracheae and in the Symphyla a very simple tracheal system opens through a single pair of spiracles situated on the head. However, Tillyard's reference to the tracheal system of the Protura as a very primitive type hardly agrees with the evidence. More probably it represents a greatly reduced system of the segmental type wherein most of the body segments had a pair of spiracles. In the Protura the tracheae open entirely through two pairs of thoracic spiracles, but it is to be noted that of the three families of the Protura, the tracheae are wanting in the two that are most specialized. Thus, the course of evolution is indicated. The proturans without tracheae are the most specialized, not the most generalized as would be required by Tillyard's theory.

(c) The Symphylian Theory. Of the several theories of the origin of insects the Symphylian Theory is the one that has been most acceptable to the writer (Ewing, 1940). According to this theory the winged insects, or Pterygota, have been derived from symphyliid, or symphyliid-like ancestors through apterygotan insects of the order Thysanura. Packard (1873, 1881) did much to establish the Symphylian Theory, but it appears that Menge (1851) was the first to demonstrate the phylogenetic importance of symphyliids. Ryder (1880), a contemporary of Packard, named the order Symphyla and subsequently gave Menge credit for first demonstrating the true phylogenetic position of symphyliids. Ryder (1881) states: "Since the publication of my notice above referred to (Ryder, 1880), I have met with a paper unknown to me at the time mine was written, which in many respects anticipates the observations

made by the writer * * *." Ryder then quotes (in English) several paragraphs from Menge's German text, the following sentence being significant; "I believe, accordingly, that *Scolopendrella* may be regarded as the type of a genus or family intermediate between the six-footed *Lepismidae* and the *Scolopendridae*." Ryder (1880), when he named the order Symphyla, stated: "I name the new group *Symphyla*, in reference to the singular combination of myriapodous, insectean and thysanurous characters which it presents."

This theory was further supported by the work of Silvestri (1901, 1907), who found, in the then recently discovered dipluran genus *Projapyx* Cook, that the jointed cerci served as outlets for spinning organs homologous with those of *Scolopendrella* and of many diplopods. Later Silvestri himself described the dipluran genus *Anajapyx*, which is even more nearly related to the Symphyla. In recent years Imms (1936) and Snodgrass (1938), in particular, have brought together much additional evidence in favor of the Symphylian Theory.

Those who reject the Symphylian Theory of the origin of Insecta on the grounds that insects are opisthogeneate while the symphyliids are progoneate may be a bit illogical. Actually the position of the genital opening in the Collembola is nearer to that in the Symphyla than it is to the position of the genital opening in the hexapod group Protura, yet students of the phylogeny of the Insecta hold that all insects have had a common origin. In the Collembola the genital opening is on the eight postcephalic segment, in the Symphyla on the fourth, and in the Protura between the fourteenth and fifteenth. Thus the genital opening in the Collembola is only four segments from its position in the Symphyla, while it is six or seven segments from its position in the Protura. Can we not, without being illogical, regard the Collembola as being progoneate, since the genital opening in this group is anterior to the sixth abdominal segment, which holds the middle position in the abdomen of a generalized insect?

THE GENERALIZED MANDIBLE OF THE DIPLOPODA.

The mandible in Diplopoda shows much variation, but in its more generalized state consists of a large basal part and a heavily sclerotized and marginally toothed, movable, distal part. The basal part usually is divided by a transverse suture into two sclerites, called by some authors the cardo and stipes and believed by them to be homologous with parts of the maxillae having the same names. Since the distal part is supplied by its own muscles and is movably articulated with the basal part, it must represent functionally a true segment. A study of the muscles of the basal part, according to Snodgrass (1928), shows

apparently that the two sclerites correspond to the cardo and stipes of the maxilla and, if so, probably do not represent distinct segments.

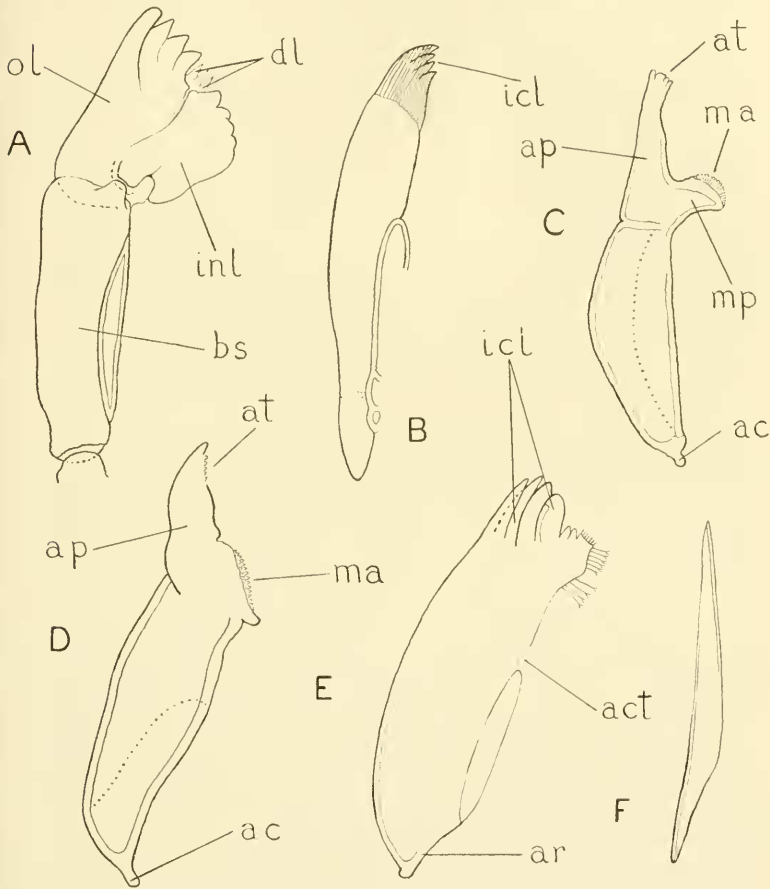


FIG. 1.—Types of mandibles found in the Symphyla and Apterygota. Dorsal view of each, not equally enlarged: *A*, Of *Hanseniella* sp., a symphyliid (original); *B*, of *Heterojapyx gallardi* Tillyard, a japygid (after Snodgrass); *C*, of *Corethromachilis brevivalpis* Carpenter, a machilid (after Carpenter); *D*, of *Cremastoccephalus pallidus* Carpenter, a springtail (after Carpenter); *E*, of *Ctenolepisma urbana* Slabaugh, a lepismatid (original); *F*, of *Acerentulus confinis* (Berlese), a proturan (after Berlese). Abbreviations: *ac*, Articulating condyle; *act*, shallow acetabulum; *ap*, apical process; *ar*, articulating ridge; *at*, apical teeth; *bs*, basal segment; *dl*, dentate lamella; *icl*, incisor lobe; *inl*, inner lobe; *ma*, molar area; *mp*, molar process; *ol*, outer lobe.

THE MANDIBLE IN SYMPHYLA.

In the Symphyla the mandible (Fig. 1, *A*) is clearly two-segmented. The basal segment is long and narrow and appears to form a part of the lateral wall of the head. It is articulated with the cranium by means of a broad groove-ridge type of hinge, the groove being on the mandible and the ridge, which in some species might be called a condyle, on the cranial margin. The distal segment is short and broad and bears large and small teeth modified chiefly for cutting and tearing. This segment is divided longitudinally by an indistinct groove or suture and has toward the middle of its anterior, toothed margin a conspicuous notch. In this notch is situated a very small sclerite that bears a few minute, sharp teeth. It has been called the dentate lamella and is regarded by some authorities as homologous with the much larger and differently formed prostheca of the members of the dipluran family Projapygidae.

The distal segment of the symphyliid mandible is hinged in a peculiar way to the proximal segment and has not been properly described by previous workers. The two segments have a three-point or tricondylic joint (Fig. 1, *A*), two of the condyles, or articulating processes, being on the base of the distal segment and one on the apex of the proximal segment. One or more of these heavily sclerotized articulating processes have been figured by others as if they were sclerites. Only by dissection and staining can their true nature be detected.

EVOLUTION OF THE INSECTEAN MANDIBLE.

Within the Symphyla and the Apterygota alone can be noted the major aspects of the evolution of the insectean type of mandible (a process well described by Snodgrass, 1935, and others). In the Symphyla (Fig. 1, *A*, *bs*) the plate-like sclerites of the basal segment of the diplopod mandible have already become anchylosed, yet the mandible as a whole is clearly two-segmented, very long, and hinged to the cranium only at its base. In the Diplura (Fig. 1, *B*) the whole mandible is consolidated into a single segment and has its proximal end cone shaped and fitting into a funnel-shaped socket on the head. In the Machilidae (Fig. 1, *C*) and the Collembola (Fig. 1, *D*) a definite articulating condyle which fits into an acetabulum on the cranium has been developed at the basal end of the mandible; and in addition an inner, subapical grinding surface, the molar area, has appeared. Finally, in most of the Lepismatidae a second articulation with the head (Fig. 1, *E*, *act*) has been attained, thus forming a mandible typical of the generalized pterygotan insects except for the depth of the acetabula, the prominence of the articulating processes, and its shape, which is considerably longer and less flattened than the mandible of

the grasshoppers, roaches, and most of the generalized pterygotans.

THE NUMBER OF THORACIC SPIRACLES IN APTERYGOTA AND THEIR POSSIBLE PHYLOGENETIC SIGNIFICANCE.

In the apterygotan hexapods there are two series of thoracic spiracles, a dorsolateral and a ventrolateral. The dorsolateral spiracles are confined to the mesothorax and metathorax, each being situated in the pleural membrane above the leg base. The ventrolateral spiracles, which are more commonly absent, are usually found on the mesothorax and metathorax. However, the first pair of the ventrolaterals may be shifted from their normal position to the posterior part of the prothorax. These ventrolateral spiracles, although situated in the pleural area, are not so closely associated with the subcoxal sclerites of the leg base as are the dorsolateral spiracles. In the Campodeidae the second pair of the ventrolateral spiracles is missing and in the Protura both pairs of ventrolateral spiracles are missing.

Since nearly all the arthropods possessing trachae have no more than a single pair of spiracles to a body segment, it is of particular importance to know why there are two pairs on a single segment in some of the thysanurans. To explain properly the origin of an additional pair of spiracles on a single thoracic segment, we should begin with a spiracular tracheal cluster served by a very short, dichotomous trunk. A further shortening of this trunk to the point of obliteration would give each branch a separate opening into the atrium of the spiracle. This process can be observed in some arthropods today. The shifting apart of these two openings, accompanied by an elongation of the atrium, should be the next step. Finally, the much elongated atrium becomes constricted and then transversely divided into two atria each having its own trunk and cluster of tracheal branches.

It is a matter of importance from the standpoint of phylogeny to know, if possible, which of the four pairs of thoracic spiracles found in the Japygidae persist in pterygote insects. That the ventrolateral mesothoracic spiracles represent the first thoracic pair in the Pterygota is indicated by their position, by the fact that they usually are better developed than the other thoracic spiracles, and by the further fact that they nearly always are present in insects known to possess thoracic spiracles, and finally because they tend to migrate into the prothorax in the Aapterygota, just as they do in the Pterygota.

In the Campodeidae the ventrolateral spiracles of the metathorax have been lost, whereas the dorsolateral pairs of the mesothorax and metathorax persist. These two latter pairs

are in exactly the same position as the only known spiracles in the Protura and in a somatic position analogous to that of the abdominal spiracles of the pterygote insects. However, since the first dorsolateral pair of thoracic spiracles is evidently lost in pterygote insects, one is led to believe that possibly the second pair may also have been lost, yet the evidence presented by the present conditions in the Campodeidae indicates otherwise.

THE NECK SPIRACLES OF COLLEMBOLA.

Tillyard (1930) not only would derive the arthropods from a primitive atracheate type, but he also held that the most primitive Insecta had no tracheae, and that the tracheal system of the Collembola, far from being of a very degenerate type, really is of a very primitive type. He states: "I submit that, if the Collembola were descended from tracheate forms, any type which now possessed a tracheal system would not have been the most highly specialized type, but one of the more primitive forms; nor would the tracheae have been in the head, but in some segment which would have clearly indicated a reduction from the original postcephalic segmentation system, as exhibited for instance in the more primitive *Thysanura* or *Pterygota*."

Nearly all the springtails are without spiracles, but a single pair is found in the sides of the neck close to the head in certain members of the family Sminthuridae and in the genus *Actaletes* Giard, a genus of questionable position. Although these spiracles have been considered as the prothoracic pair by Davies (1927), Snodgrass (1935) has pointed out that they really "lie in the region of the second maxillary segment," hence probably represent "persisting examples of the second maxillary spiracles, known otherwise only as temporary tracheal openings in the embryo of the honey bee."

In this connection it should be noted that in the Symphyla the only pair of spiracles present is a head pair. Each spiracle of this head pair usually is situated in the membrane between the base of the mandible and the epicranium, but in some species the spiracle and a part of the tracheal trunk have become included in the sclerotization of the basal segment of the mandible. For this reason this pair of spiracles should be known as the mandibular pair. Their position, so much more anterior to that of the so-called head spiracles of Collembola, indicates that they are not homologous with the latter. The presence in several groups of arthropods of spiracles situated near or upon the mouth parts indicates that primitive arthropods probably had a pair of tracheal invaginations on each appendage-bearing segment of the head.

TYPES OF ANTENNAE IN INSECTS AND IN THEIR
NEAR RELATIVES.

Some differences of opinion have long existed among entomologists relative to the number of true segments in the antennae of various groups of insects. In most groups the antenna has been recognized as typical for all insects and composed of the following: A large basal segment, the scape, articulated to the epicranium at a single point, followed by a somewhat smaller subsegment, the pedicel, which bears distally a long whiplike terminal flagellum marked by many annulations. Such an antenna evidently should be regarded as composed of only two true segments. In various groups different workers have reported the occurrence of muscles in segments of the antenna beyond the first, but their findings have not been generally accepted.

The whole matter of segmentation of the antennae in insects and other arthropods has been recently thoroughly investigated by Imms (1939). As a result of these investigations he concludes that, "The first antennae of arthropods are divisible into two main types, viz. (1) segmented antennae and (2) annulated antennae." In the first type the antenna is composed of a variable number of true segments, each being supplied by one or more muscles. In the second type the antenna is composed of a basal peduncle, consisting of one or more true segments, and a distal annulated flagellum or pair of flagella.

Among the outstanding facts apparently established by Imms was his demonstration that in the "Thysanura Entognatha" the antennae are of the first type (Fig. 2), having many true segments; while, in the "Thysanura Ectognatha" and all the Pterygota the antennae are of the second type, having a true basal segment and a distal annulated flagellum.

Another important result of Imms' work was his demonstration that in all the Collembola only four true segments are to be found in the antennae. In the genus *Orchesella*, where the antennae have been regarded as six-segmented, he showed that, according to the musculature, the first and second antennal segments are each divided into two false segments or subsegments. He found that the first and second segments each contain a levator, a depressor, and an extensor muscle for moving the approximate distal segment. The third antennal segment, according to Imms, contains only a levator and a depressor for moving the distal segment, which is without contained muscles. The muscles contained in the first and second segments are very weak and slender.

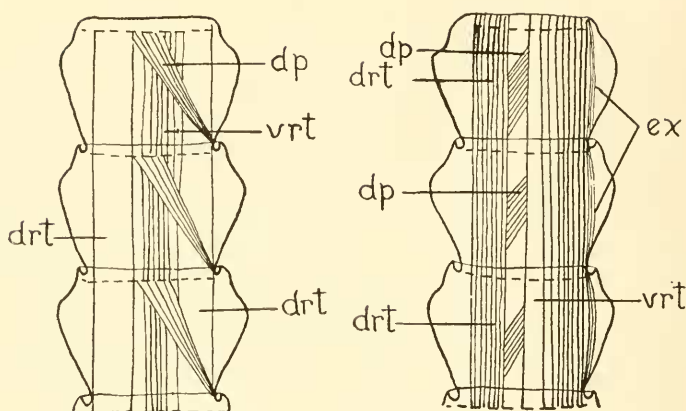


FIG. 2.—Antennal segments VIII to X of a species of *Japyx*; to the left, ventral view; to the right, dorsal view; *dp*, depressor muscle; *drt*, dorsal retractor muscle; *ex*, extensors; *vrt*, ventral retractor muscle. (After Imms, 1939.)

I have examined many mounts of Collembola, some of which show the muscles in good condition, and find a corroboration of most of the claims stated by Imms. In one species, *Aphorura ambulans* (Linn.), the muscles in the second and third segments are large and conspicuous while in another species, *Tomocerus arcticus* Sch., no muscles were detected in the third segment, although they were unusually well developed in the second, showing clearly the cross striations which easily identify muscle fibers. It should be stated that in this species, the third segment is excessively long, being longer than the other three segments combined, and annulated throughout.

Could not the arthropods with the antennae of the first type, as given by Imms, be further divided into two major groups, (1) those in which the antenna is composed exclusively of a large and indefinite number of true segments, and (2) those in which the antenna is composed of a definite, small number of true segments, but may also possess annulations? If this division is made, it gives the following grouping:

Under (1): Diplopoda, Chilopoda, Symphyla, "Thysanura Entognatha," and certain crustaceans.

Under (2): Pauropoda and Collembola.

FOSSIL APTERYGOTANS.

The most ancient fossil apterygotan, according to Tillyard (1928), is a collembolan found in Lower Devonian peat bogs. The species is represented by only a few head fragments, which contribute nothing to our knowledge of the relationships of the group, yet the finding of an insect in such ancient rocks is a matter of much importance.

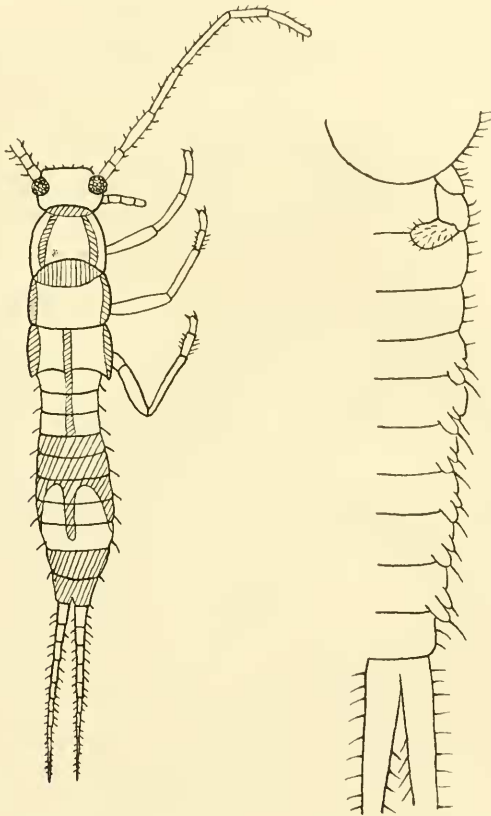


FIG. 3.—*Ocellia articulicornis* v. Olfers, a diplurid in fossil amber; at left, dorsal view; at right, ventral view of left half of abdomen. (After v. Olfers, 1907.)

In general, but few fossil apterygotans have been found, and most of them were in amber. Some of these, however, have been well described and figured. For the most part they represent species belonging to modern genera or to genera closely

related to modern genera. Two of the species are unusual because they exhibit characters of considerably phylogenetic importance. The first is the type of the genus *Ocellia* established by Olfers (1907). This species, *O. articulicornis* (Fig. 3), is represented by two specimens and is quite remarkable in that it has the characters of both the Diplura and Triplura. Because of the presence of but two caudal appendages it is placed in the Diplura, but a new family is created for it. According to Olfers (1907) this species (Fig. 3) is about five millimeters long. In general it has the appearance of a campodeid, but it has the hypognathous head, the long maxillary palpi, and the compound eyes of a lepismatid. The antennae are intermediate in character between the true pterygotan type of most of the Triplura and the long beaded type, typical of the Diplura. The two-segmented tarsi also are intermediate in character between the unsegmented tarsi of the other diplurans and the typical three-segmented tarsi of the triplurans. The thorax, with its three

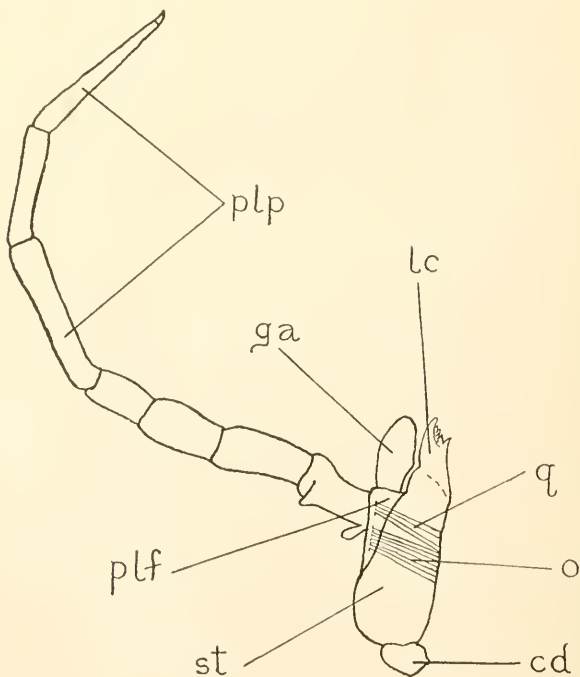


FIG. 4.—Maxilla of a machilid, *Nesomachilis* sp., *cd*, cardo; *ga*, galea; *lc*, lacinia; *o*, levator muscle of palpus; *plf*, palpifer; *plp*, maxillary palpus; *q*, depressor muscle of palpus; *st*, stipes. (Adapted from Snodgrass, 1928.)

subequal, freely articulated segments, is like that found in the subfamily Maindroniinae, of the family Lepismatidae.

The other fossil apterygotan of particular interest is a collembolan, described by the late J. W. Folson (1937) from Canadian amber. He described it as *Protentomobrya walkeri* and erected for it a new family, the Protentomobryidae. This collembolan is remarkable in not having a true spring or furcula but being provided instead with a pair of slender, diverging stylets, each swollen basally. Except for this peculiar character, *P. walkeri* would be placed in the family Entomobryidae. That it is a more primitive form connecting the Entomobryidae with the remainder of the Collembola is evident.

INTERRELATIONSHIPS OF SOME OF THE GROUPS OF PRIMITIVE INSECTS.

In recent years morphologists, as a result of a more intensified study of some of the common and larger species of apterygotans, have emphasized points of their apparent disunity. Particularly have they been inclined to break up the old group Thysanura into two orders or subclasses, to which the names Entognatha (= Entotropha) and Ectognatha (Ectotropha) have been given. Thus, on the basis of a study of the mandibles, the Lepismatidae have been regarded as having the two-hinged insectean type, and to be closely related to the Pterygota; while the Machilidae, with a single-hinged mandible, are to be placed in a lower category with other apterygotans.

Also the Lepismatidae have been regarded as having the true insectean type of antenna, with a basal segment, followed by a subsegment bearing a multiannulated flagellum, while the Entognatha are observed to have the long, beaded type, with an indefinite number of true segments.

While such conclusions are warranted by a study of the more common forms of Apterygota, yet some of the smaller and rarer species show characters that are intermediate and in a way connect these groups that appear to be so diverse. Thus, while it is true that the mandibles of the typical members of the Lepismatidae are two-hinged and similar to those of pterygote insects, yet in some genera there is no articulating condyle at the basal hinge, as is found in most insects, but a ridge. Further, the anterior, or more distal, articulation in some genera is so primitive as to be represented merely by two thickened pressure points of the integument, there being no socket or process.

The distinction made between the Lepismatidae and most other primitive insects, on the basis of their antennae being of the pterygotan type with a scape and a long, annulated flagellum, is not so sharp when some of the rarer members of the sub-

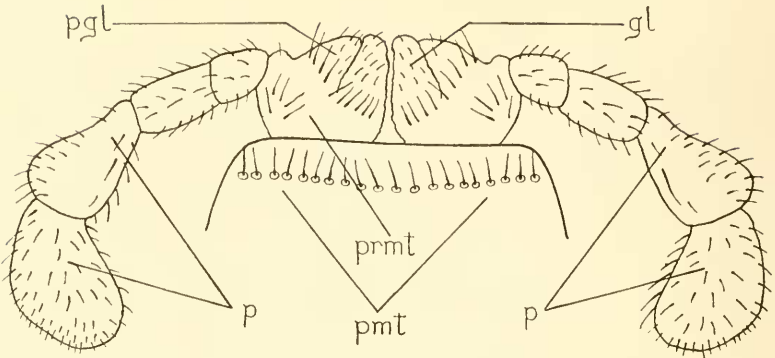


FIG. 5.—Ventral view of labium of lepidisomatid, *Ctenolepisma longicauda* Escherich; *gl*, glossa; *p*, labial palpi; *pgl*, paraglossa; *pmt*, postmentum; *prmt*, prementum. (Adapted from Escherich, 1905.)

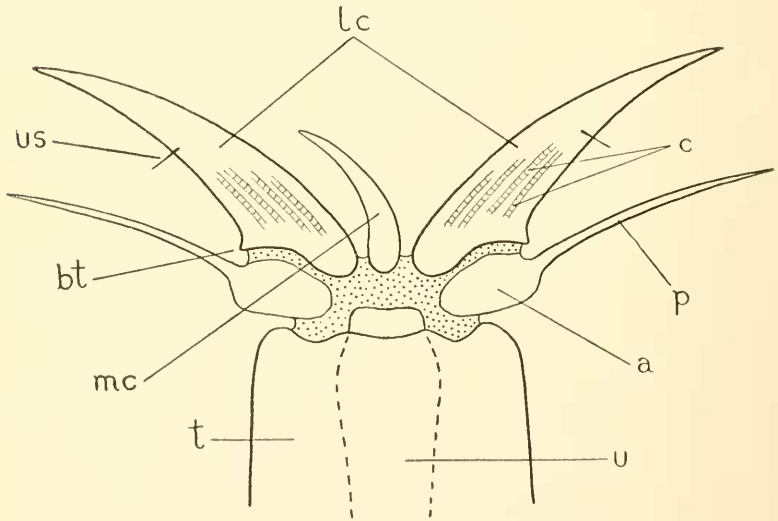


FIG. 6.—Ventral view of pretarsus and end of tarsus of a campodeid (family Campodeidae) with terminology for different parts (semidiagrammatic); *a*, auxilia; *bt*, basal tooth of lateral claw; *c*, canaliculae; *lc*, lateral claws; *mc*, median claw (arolium); *p*, setalike pulvillus; *t*, tarsus; *u*, unguis; *us*, unguis seta.

family Maindroniinae are considered. Some of these (Fig. 7) have antennae of the beaded type as found in the Diplura.

Those who divide most of the apterygotan insects into two groups, the Entognatha and the Ectognatha, emphasize a

character which in most species is easily detected yet in others is ascertained with difficulty. Actually there is a great variation in the degree to which the mouth parts have been infolded, and the deeper significance of such infolding, such as it is, has not been properly understood. The writer has noted that the type of mandible present in the Japygidae, with its long, unsegmented shaft and cone-shaped basal end articulating with a funnel-shaped socket in the head, is repeated in some of the Collembola

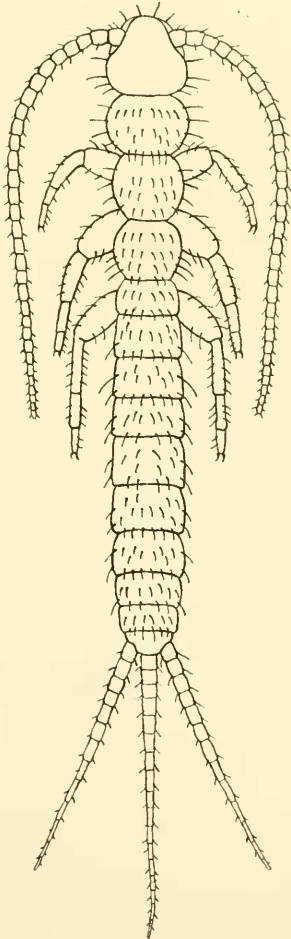


FIG. 7.—*Trinemophora michaelsoni* Schäffer, a lepismatid, with several diplurid characters. (After Escherich, 1905.)

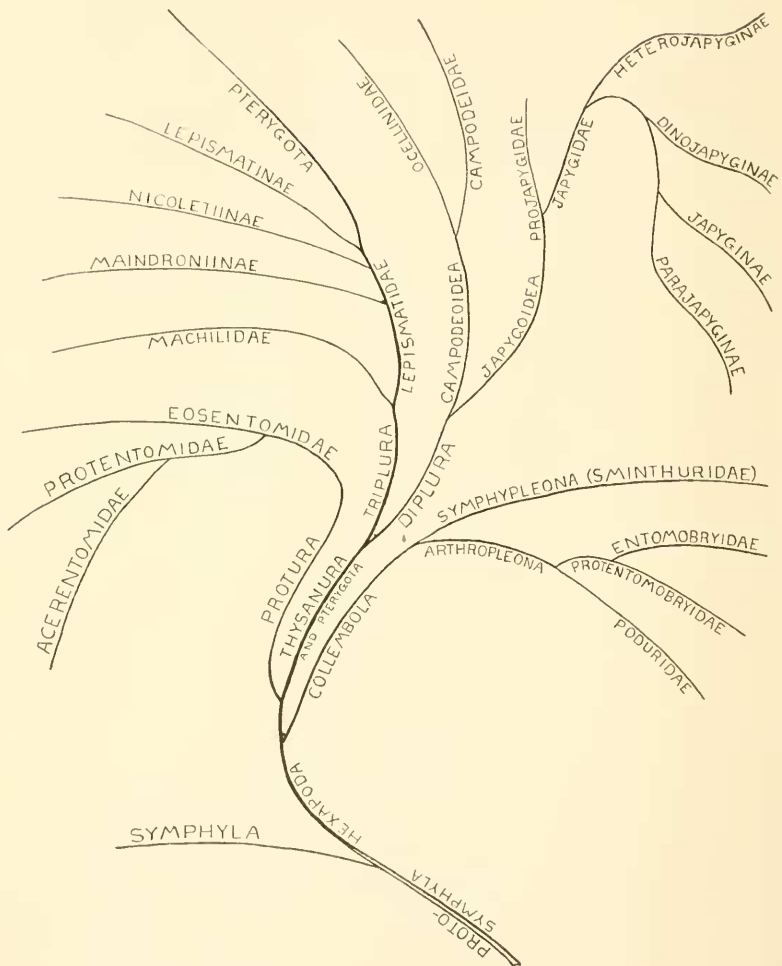


FIG. 8.—Phylogenetic tree indicating the suggested origin of the Apterygota and the derivation and relationships of its various subgroups.

which are entognathous, yet the mandibles of certain other collembolans (Fig. 1, *D*) have a typical articulating condyle.

While most of the members of the family Lepismatidae have the characters with which entomologists in general are familiar, yet those of *Trinemophora* (Fig. 7) are strangely mixed with those of members of both the old groups, Ectognatha and Entognatha. This is well displayed in Escherich's figure of

Trinemophora michaelsoni Schäffer (Fig. 7). Although this species is a lepismatid and a tripluran it has the following diplurid characters: The general shape of the body, which is campodeiform, the prognathous head, the absence of eyes, the beaded antennae, the absence of body scales, and a thorax with subequal, freely articulated segments. It is further noted that the two-segmented tarsi represent an intermediate condition between the old groups Ectognatha and Entognatha.

THE FAMILIES AND SUBFAMILIES OF COLLEMBOLA.

As compared to the Thysanura, the Collembola are more homogenous and undoubtedly constitute a more compact natural group, yet apparently because of their large numbers and extremely wide distribution, they have been placed in several families and many subfamilies. The numbers of both of these are here much reduced. The family Actaletidae Handlirsh, based on the genus *Actaletes* Giard, probably is not well founded. In *Actaletes* the head is hypognathous, with the antennae situated in the middle, and the last three abdominal segments are fused. Further, it is claimed that cephalic tracheae are present and the gonads are of unusual shape. The head characters here mentioned would apply equally to *Podura* and the fusion of the last three abdominal segments is not restricted to *Actaletes*. Lastly, the claims of the presence of cephalic tracheae and the peculiarities of the gonads need further confirmation. If this family is to be recognized as a subfamily it should come next to the Isotominae in the family Entomobryidae. The family Neelidae Folsom differs but slightly, due to intergrades, from the Sminthuridae. Its retention as a subfamily possibly is indicated.

KEY FOR THE CLASSIFICATION OF CERTAIN PRIMITIVE ARTHROPOD GROUPS, INCLUDING THE APTERYGOTA.

- A. Body divided into 2 regions, a head, consisting of the consolidation of the preoral segments plus the first 4 postoral segments, and a chain of freely articulated segments; genital opening farther forward than the fifth postcephalic body segment.
- B. Body region composed of 12 segments, and with most of the terga fused into couples, their number being less than that of the 9 evenly spaced legs; first body segment with vestigial appendages; head hypognathous; antennae branched at apex of fourth segment; mandibles unsegmented; genital opening on third postcephalic body segment ... *PAUROPODA* Lubbock
- BB. Body region composed of more than 12 segments, and with none of its terga fused into couples, number of terga greater than that of the 12 pairs of legs usually present (the first pair may

- be either reduced or absent); head prognathous; antennae not branched; mandibles 2-segmented; genital opening on fourth postcephalic body segment.....*SYMPHYLA* Ryder
- AA. Body divided into 3 regions, a head, composed of the preoral and first 4 postoral segments, a leg-bearing thorax, composed of the first 3 postcephalic segments, and an abdomen composed of a chain of 6 to 12 segments; genital opening farther back than seventh postcephalic segment.
- B. Dorsum of head frequently showing a series of transverse sutures possibly indicating its division into primitive terga; antennae absent; mandibles lancetlike, toothless, protrusible; pretarsi with a single claw; abdomen with 12 segments in adult, a single segment being added during each molt of immature individual; abdominal appendages absent from segments behind the third; genital opening between sterna XI and XII.....*PROTURA* Silvestri
- BB. Dorsum of head never showing a series of transverse sutures; antennae present; mandibles usually with teeth and adapted for chewing; pretarsi in adults with 1 to 3 claws each; abdomen never with more than 11 segments and no segments added after embryonic stage; abdominal appendages may be on any segment; genital opening never farther back than membrane between sterna IX and X.
- C. Abdomen composed of 6 segments in all instars, including the embryo; 2 or more adjacent segments frequently partially or entirely anchylosed; segment I with a median ventral appendage in the form of a tube; II usually with a short, greatly modified ventral appendage; IV usually with a forked appendage used for jumping; total cleavage taking place in embryonic development; antennae composed of 4 true segments, but segments I and II each may be divided into 2 subsegments and III and IV into many annulations; mandibles usually present and adapted for chewing, rarely reduced to stylets or absent; tracheae, when present, without anastomosis and opening through a single pair of spiracles on the neck; malpighian vessels absent; tarsi very short, or absent (probably being fused with tibiae).....*COLLEMBOLA* Lubbock
- CC. Abdomen composed of 10 or 11 freely articulated segments; appendages of no pair fused into a tube or forming a forked, median appendage; antennae composed of a large number of true segments or a basal true segment and many annulations; mandibles always present and adapted for cutting or chewing; tracheae opening through spiracles situated farther back than the neck; malpighian vessels sometimes present, but poorly developed; tarsi not reduced or fused with tibiae.....*THYSANURA* Lubbock

KEY FOR THE CLASSIFICATION OF THE FAMILIES AND SUBFAMILIES OF PROTURA.²

- A. Tracheae present and opening through 2 pairs of spiracles, 1 on mesothorax and 1 on metathorax; abdominal segments I-III each with a pair of 2-segmented appendages; abdominal combs absent
EOSENTOMIDAE Berlese
- AA. Tracheae absent; abdominal segment III with a pair of unsegmented appendages; a pair of abdominal combs usually present on segment VIII.
- B. Abdominal terga without transverse lines or sutures or laterotergites but each with 1 complete, transverse row of setae; abdominal combs reduced or absent...*PROTENTOMIDAE* Ewing
- C. Second pair of abdominal appendages 2-segmented; abdominal combs present; tarsus I with sensory setae.....
PROTENTOMINAE Mills
- CC. Second pair of abdominal appendages unsegmented; abdominal combs absent.....*MICROENTOMINAE* Ewing
- BB. At least some abdominal terga each with 1 to 3 transverse lines or sutures, a pair of laterotergites, and 2 complete transverse rows of setae; abdominal combs not reduced.....
ACERENTOMIDAE Berlese

KEY FOR THE CLASSIFICATION OF THE SUBORDERS, SUPERFAMILIES, FAMILIES, AND SUBFAMILIES OF THYSANURA.

- A. Mouth parts withdrawn into the head; antennae usually divided into many true segments none of which is annulated; mandibles each articulating with head by means of its cone-shaped proximal end fitting into a funnel-shaped socket; tarsi usually simple, never divided into more than 2 subsegments; abdomen provided with only 2 caudal appendages (cerci).....
DIPLURA Börner (= *THYSANURA ENTOTROPHA* Grassi)
- B. Tracheal system with longitudinal connecting trunks between adjacent spiracular trunks; thoracic spiracles, when unreduced in number, 4, a dorsolateral and ventrolateral pair on each of the last 2 segments; abdominal spiracles, when unreduced, 7, 1 pair on each of first 7 segments; pretarsal claws without dorsal foliaceous expansions; cerci stout, relatively short
JAPYGOIDEA, new superfamily
- C. Cerci segmented, straight, tapering, each bearing apically the opening of a duct from spinning glands; mandible with prostheca (inner, subbasal appendix); abdominal segment I with 2 pairs of appendages; segment IX of abdomen not greatly shortened but similar to the other segments; female with 2

² The keys for the classification of the different groups of Apterygota that are presented in the following pages have been based in part or largely upon the work of the following: Protura, Ewing (1940); Japygidae, Womersley (1939); Machilidae, Verhoeff (1910); Lepismatidae, Escherich (1905), and Collembola, Mills (1934).

- pairs of ovaries situated in abdominal segments IV to VI;
6 very short malpighian tubes present *PROJAPYGINAE* Cook
- CC. Cerci unsegmented, modified into a pair of hooked pincers;
spinning glands absent; mandible without prostheca; abdominal segment I with 1 pair of appendages in addition to a pair of seta-bearing subcoxal organs; segment IX of abdomen greatly shortened and modified so as firmly to join with the lengthened and heavily sclerotized segment X; female, in some species at least, with a pair of simple ovaries in each of abdominal segments I to VII; malpighian tubes vestigial or absent.....*JAPYGINAE* Lubbock³
- D. Antennae with sense-setae on some of the segments.
- E. Antennae with sense-setae on other segments in addition to IV to VI.
- F. Sense-setae on antennal segments IV to XIII; labial palpi present; body almost naked above; pretarsi each with a middle claw; spiracles on abdominal segment VII very oblong and greatly enlarged
HETEROJAPYGINAE Womersley
- FF. Sense-setae on antennal segments IV to XX; labial palpi wanting; body and appendages provided with many long, hairlike setae; pretarsi each with 2 subequal claws.....*DINJAPGINAE* Womersley
- EE. Antennae with sense-setae on segments IV to VI only
JAPYGINAE Womersley
- DD. Antennae without sense-setae; labial palpi wanting.....
PARAJAPYGINAE Womersley
- BB. Tracheal system of a primitive type in that there is no anastomosis between the tracheae opening through one spiracle with those opening through another spiracle; thoracic spiracles, as far as known, 3, a dorsolateral and a ventrolateral pair on mesothorax and a dorsolateral pair on metathorax; abdomen without spiracles; pretarsal claws frequently with a dorsal foliaceous expansion; cerci long, slender, flagelliform, marked by many annulations.....
CAMPODEOIDEA Handlirsch
- C. Head prognathous; eyes absent; antennal segments short, frequently beadlike; tarsi unsegmented; abdominal segments III to VII with appendages, VIII and IX without
CAMPODEIDAE Meinert
- CC. Head hypognathous; compound eyes present; antennal segments much longer than broad; tarsi 2-segmented; abdominal

³ The family name Japygidae is based on the generic name *Japyx*, which originally was spelled *Iapyx*. Although the emended spelling of the name has been almost universally used in recent years, justification for the emendation is to be questioned since Latin dictionaries give the spelling *Iapyx*. The word is derived from the Greek poetical name for an inhabitant of Calabria, that part of Italy forming the "toe of the boot."

segments II and III without appendages, IV to IX each with 2 pairs of appendages. Contains a single extinct species

OCELLIIDAE, new family

AA. Mouth parts not withdrawn into the head; antennae usually divided into a basal true segment, followed by a short subsegment bearing a distal flagellum composed of many annulations; mandibles with either 1 or 2 articulations to the head; tarsi divided into 2, 3, or 4 subsegments; abdomen provided with 3 caudal appendages.....

TRIPLURA, new name (= *THYSANURA ECTOTROPHIA* Grassi)

B. Body compressed, or flattened laterally; mandibles each articulating with the head by means of a condyle on its proximal end fitting into an acetabulum; tracheal system of a primitive type in that there is no anastomosis between the tracheae opening through one spiracle with those opening through another; coxae II and III frequently with a styletlike process; tarsi each with 3 subsegments, the first usually being so reduced as to permit the middle subsegment to articulate dorsally with the tibia.....*MACHILIDAE* Grassi

C. Not more than a single pair of eversible sacs on any one abdominal segment.

D. Abdominal segments II to VII with large, triangular sterna.....*PREMACHILINAE* Carpenter

DD. All abdominal sterna very small, some not visible.....

MEINERTELLINAE Verhoeff

CC. Two pairs of eversible sacs on each of 2 or more abdominal segments.....*MACHILINAE* Verhoeff

BB. Body depressed or flattened dorsoventrally; mandibles usually having 2 articulations with the head, a basal and an inner distal; tracheal system, when unreduced, with both longitudinal and transverse connecting trunks between the spiracular trunks; coxae II and III without appendages; tarsi with 2 to 4 subsegments, when with 3 subsegments, the first usually the longest, the second short and never articulating with the tibia.....*LEPISMATIDAE* Burmeister

C. Body slender, without scales, and with sides subparallel; head longer than prothorax; inner margin of maxillary lacinia smooth.....*MAINDRONIINAE* Escherich

CC. Body stouter, usually with scales, and sides seldom subparallel; head shorter than prothorax; inner margin of maxillary lacinia with teeth and setae.

D. Eyes absent; body with or without scales; subcoxae of genital segments narrow, not covering bases of gonapophyses.....*NICOLETIINAE* Escherich

DD. Eyes present; body with scales; subcoxae of genital segments broad, covering bases of gonapophyses.....

LEPISMATINAE Escherich

KEY FOR THE CLASSIFICATION OF THE SUBORDERS, FAMILIES, AND SUBFAMILIES
OF COLLEMBOLA.

- A. Body elongate, not swollen; segments of thorax and abdomen distinct from one another, except in a few cases where some of the most posterior segments of abdomen are ankylosed; antennal segments I and II each may be divided into 2 subsegments; postantennal organ may be present; sacs of ventral tube small, without warts
ARTHROPLEONA Börner
- B. Abdominal segment IV provided with a pair of long, slender stylets, but no furcula; first abdominal segment much reduced. Contains a single extinct species, known only from Canadian amber.....*PROTENTOMOBRYIDAE* Folsom
- BB. Abdominal segment IV without a pair of stylets, but usually provided with a forked appendage called the furcula.
- C. Integument smooth (rarely minutely granulate), covered with setae or scales; prothorax much reduced dorsally, without prominent dorsal setae; furcula usually present.
ENTOMOBRYIDAE Tömösvary
- D. Tergum IV of abdomen usually much longer than III; posterior abdominal segments never ankylosed.....*ENTOMOBRYINAE* Schäffer
- DD. Tergum IV of abdomen subequal to III; some of posterior abdominal segments may be ankylosed.
- E. Body scaled; antennal segments III and IV annulate; posterior abdominal segments never ankylosed.....*TOMOCERINAE* Schäffer
- EE. Body not scaled; antennal segments III and IV seldom annulate; last 2 or 3 abdominal segments may be ankylosed *ISOTOMINAE* Schäffer
- CC. Integument granulate or tuberculate, never bearing scales; prothorax much less reduced, with prominent dorsal setae; furcula frequently wanting....*PODURIDAE* Lubbock
- AA. Body short, swollen, frequently subglobose; first 4 abdominal segments, and frequently those of the thorax in addition, ankylosed, forming a single mass; neither antennal segment I nor II divided into subsegments; postantennal organs absent; sacs of ventral tube large, frequently warty.....*SYMPHYPLEONA* Börner
Contains but a single family.....*SMINTHURIDAE* Lubbock

CONCLUSIONS.

1. Only three of the several theories of the origin of insects have any important following today.

2. Since the prevailing evidence appears to be against the acceptance of the Crustacean Theory of the origin of insects, it is ill advised to use such crustacean terms as endopodite and exopodite, as well as certain others, in naming parts of an insectean segmental appendage. The use of such terms in describing

the male genitalia (of fleas, for example), as is done today by some of the leading authorities for that group, is unwarranted confusing, and not justified on the grounds of homology.

3. The distal segment of the two-segmented mandible in the Symphyla is joined in a peculiar way to the first segment by means of a tricondylic hinge.

4. Of the two pairs of mesothoracic spiracles found in the Japygidae, apparently it is the ventrolateral pair that persists in pterygote insects.

5. The so-called neck spiracles of certain Collembola probably are not of the most primitive type as has been claimed, but represent a reduction from a segmentally arranged system. This is indicated by the presence of spiracles on or near the mouth parts in arthropod groups other than the Collembola, and by the presence of maxillary spiracles in the embryo of the honey bee.

6. Although the antennae of all arthropods may roughly be regarded as belonging to two types, segmented antennae and annulated antennae, an intermediate type may be recognized for those antennae that are composed of a small but definite number of true segments, some of which may be annulated.

7. The characters of certain of the little known and of fossil species of Thysanura tend to unite the families and subfamilies of the same into a more unified group than has been granted by most students of phylogeny.

8. While the Protura and Collembola are to be regarded as groups of very ancient origin and probably should not be included in Insecta proper, yet they both have many of the characteristics of other apterygotans and some of those of the more generalized pterygotans.

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